SOIL ANIMALS IN DETRITE FOOD WEBS

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ПОЧВЕННЫЕ ЖИВОТНЫЕ В ДЕТРИТНЫХ ПИЩЕВЫХ ЦЕПЯХ

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Trophic structure of animal communities is the essential feature determining the participation of invertebrates in soil trophodynamics. The main trophic groups are consumers of microflora, saprophages directly utilizing plant remains, phytophages feeding on roots and above ground plant parts and predators. Ratios of these groups vary widely in different soil types. The trophic structure of soil animal communities is known to depend on both hydrothermal conditions, composition of the plant cover and soil features.

In this paper we analyze basic types of food webs in soils under different plant communities. Formation of different patterns of a trophic structure in soil animal communities is considered to reflect the evolution of trophic relations of soil organisms with main phylogenetic groups of plants.

Food Webs in Soil Algae Communities

Food chains are already formed on bare ground (weathering rocks, fine earth, sands etc.). Soil algae and lichens seem to be the pioneer autothrophs colonizing mineral substrates. Up to 80% of primary production is accounted for by filamentous Cyanophyta. Algal cell walls secrete abundant slime retaining the water in dry air. This explains why soil algal aggregations represent favourable microhabitats for heterothroph organisms - bacteria and small animals (Shtina, Gollerbach, 1976).

Table 1. Soil invertebrates in algal communities of the polar desert

Animal groups	Ind.m^{-2}
Nematoda	
Enchytraeidae	3-6 x 10^3
Gamasidae	50-100
Collembola	10-300 x 10^3
Chironomidae (l)	50-1500
Mycetophilidae (l)	
Trichoceridae (l)	

Special investigations of animal populations in algal communities and their trophic relations were carried out in polar desert (Cape Cheluskin, Taimyr). Algal habitats have a relative abundant animal population compared with that in moss ones (Chernov et al., 1976). The biomass of soil invertebrates averaged 3,5 $g.m^{-2}$ (Striganova, Chernov, 1980). The main groups in algal habitats were Nematoda, Enchytraeidae, Collembola and Chironomid larvae (Table 1).

Phycophages seem to predominate among nonpredatory forms. Remains of soil algae were revealed in the guts of Dorylaimids - the most numerous Dematoda group, as well as numerous representatives of Collembola (11 species) and larvae of Diptera. Algal production is utilized and its remains mineralized very actively. Due to that the peat formation was not recorded even under unfavourable conditions of a polar desert.

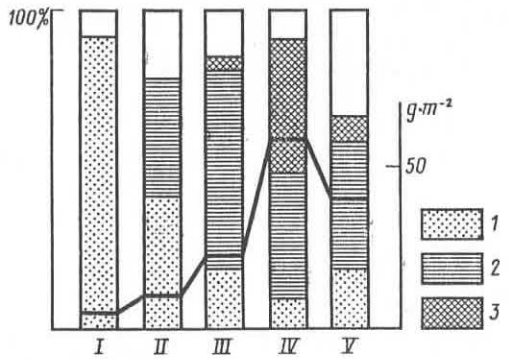
Animal populations in primitive rock soils were investigated in the Caucasus and Ural mountains (Stebaev, 1958, 1963). Collembola and Enchytraeida were found to predominate during the pioneer algal stage of plant successions.

Grazing food chains based on algae seem to prevail in pioneer communities on bare ground. This feature allows to consider them as a counterpart of planctonic communities transferred into the land conditions. The majority of animal groups in algal habitats have either aquatic ancestors or closely related aquatic forms, for example, Enchytraeidae, Chironomidae larvae.

Soil algae with a peculiar animal population often colonize dry mineral substrates. Longevity of their life depends on atmosphere moisture. Activity of algal communities seems to be ephemeral. Many invertebrate forms characteristic of these microhabitats are r-strategists. The planctonic-like trophic structure is proposed to be characteristic of pioneer invertebrate communities, which initially colonized the terrestrial environment in the course of evolution.

Trophic Relations in Soils of Moss Habitats

In the course of a primary soil formation the algal cover changes into a moss-lichen one. Moss communities are widely distributed in the tundra zone and bog ecosystems. Invertebrate populations of moss habitats are very abundant (Table 2). Among different trophic groups microphytophages constitute about 40% for the zoomass. Detritophages are also numerous (Fig.).



Biomass of invertebrates in zonal soil types and ratios of different trophic groups in saprophilic complexes

I – polar desert, II – moss tundra habitats, III – coniferous taiga forest, IV – oak forest, V – meadow steppe; 1 – microphytophages, 2 – detritophages, 3 – primary decomposers (saprophytophages)

T a b l e 2. Soil invertebrates in moss habitats

Animal groups	Taimyr Peninsula		Karelian
	arctic tundra	tundra bog	moss bog
	after Chernov, 1978		after Kozlovskaja, 1976
Nematoda	$1.7 \cdot 10^6$	$0.8 \cdot 10^6$	
Enchytraeidae	800	100-200	106-2300
Lumbricidae	5	0-10	-
Gamasidae	3160	500-3200	
Oribatei	4500	100-4000	660-766
Collembola predatory	4400	8700-32700	1500-4500
Coleoptera	20	2-40	3-5
Tipulidae (l)	2	29-50	
Diptera (l) oth.	30	80-40	

Many soil invertebrates use green moss tissues for food. It includes members of Collembola, Oribatei and Tipulid larvae (Striganova, 1978, 1980).

Food preferences were investigated with special reference to Tipula carinifrons Schumm. (Diptera: Tipulidae) and Eisenia nordenskioldi (Eisen)(Lumbricidae), numerous in tundra communities. Tipulid larvae are known to utilize mosses. Feeding of T.scripta on Sphagnum was described by Smirnov(1958). In our investigations remains of green mosses were recorded in the guts of T.carinifrons. Their utilization efficiency averaged 80%. These insects have evidently symbiotic microorganisms which degrade polysaccharides in moss tissues. But the latter and litter of seed plants constitute a minor part of the gut content. Soil algae seem to be the main food resource. In arctic tundra habitats, where vascular plants were absent, T.carinifrons were observed to feed only on soil algae (Striganova, 1978).

E.nordenskioldi preferred heavily decomposed grass detrite enriched by microflora. Digestion rates of the detrite averaged 13-14 hours, which was 2-3 times longer that as in conspecific populations from the temperate zone (Striganova, 1984). Soil algae play a significant role in the feeding of E. nordenskioldi in the tundra zone. Near the northern limit of their range (Northern part of the arctic tundra subzone) these earthworms exclusively switch over to the algal diet. We observed them feeding on Nostoc commune(Cyanophyta).

Soil algae are actively consumed by both microphytophage and detritophage groupings. They are readily digested, have high nutritive qualities and are abundant in moss habitats. Moss sod has a high capacity to water retention. The moist atmosphere at the soil surface under moss cover promotes the development of algae. Production of soil algae in bogs reaches 2-8 $g \cdot m^{-2}$ and that of mosses varies between II and 300 $g \cdot m^{-2}$ (Shtina et al., 1981, Alexachina, Shtina, 1984). In Ireland's bogs the algal biomass averages 186 $g \cdot m^{-2}$ and the moss one only 50 $g \cdot m^{-2}$ (Moore et al., 1975). Hence, the values of algal and moss biomass indices are comparable, and thus, the algal production in moss communities can maintain an intensive energy flow along food chains.

Many soil invertebrates retain trophic relations with algae. The proportion of algae in the diet of saprophilic animals was observed to increase under more unfavourable conditions. The role of invertebrates as direct consumers of both living and dead moss tissues is low. Moss remains are degraded by microflora (Frankland, 1974). Animals are involved in detrite food chains based on moss litter as consumers of saprotroph microorganisms. Low level of the microbial activity, rates of mineralization of moss remains results in the accumulation of uncompletely degraded organic matters and peat formation

Soil Food Webs in Seed Plants' Communities

The active contribution of soil animals to detrite food chains is characteristic of soils under seed plants' communities. Trophic structure of animal populations has received most attention with special reference to forest soils. The breakdown of plant remains in coniferous and deciduous forests is done by special saprophilic complexes of soil invertebrates envolved in detrite chains at different trophic levels.

Microfungi seem to be the most significant primary decomposers of coniferous litter in taiga forests. They provide food resources for many invertebrates: Oribatid mites, Collembola and Enchytraeidae, predominating in animal populations of the taiga zone. The biomass of microarthropods averages 4.5 $g \cdot m^{-2}$. The majority of microarthropods are the specialized mycophages, selective in relation to particular groups and species of fungi, ages of mycelia, vegetative and generative structures etc. (Striganova, 1980). The activity of mycophages prevents aging of fungal mycelia, accumulation of acid metabolites of fungi in the soil, which may change a dynamic of soil processes unfavourably.

Coniferous fall is undigestible for many saprophages. It is known to be utilized by separate groups only, e.g. Phthiracarid mites. But detritophages use heavily degraded coniferous litter, leached and enriched by microorganisms. Lumbricids, feeding in mineral soil horizons represent the most active group: their biomass in taiga forest soils averages 16.5 $g \cdot m^{-2}$ (70% of the whole zoomass) (Fig.). High invertebrate activity in the decomposing litter promotes microbial successions and accelerates mineralization rates. In coniferous litter weight loss reaches 40-50% in two years.

Angiosperm communities are characterized by the presence of primary decomposers among soil animals. Typical representatives of this trophic group are Diplopods, Isopods, Tipulid and Bibionid larvae, some species of Lumbricids feeding in the litter layer. Some forms were reported to have polysaccharides degrading enzymes (Tracey, 1951, Striganova, 1970, Kozlovskaja, Striganova, 1977). Population densities of primary decomposers are especially high in deciduous forests and meadow steppe: numbers of Lumbricidae average 500 and 114 $Ind.m^{-2}$ respectively in comparison with 20 $Ind.m^{-2}$ in taiga coniferous forests. Numbers of Diplopods reach 130 $Ind.m^{-2}$ in broadleaved forests and 80 $Ind.m^{-2}$ - in meadow steppe, what is 8-10 times as high as in taiga soils. Primary decomposers were estimated to utilize up to 13 $g \cdot m^{-2}$ of leaf litter per day in oak forests of the Russian Plain. Under favourable conditions the invertebrates' activity determines the rates of decomposition processes. Mineralization rates of the Angiosperm litter are higher by an order that those in Gymnosperm communities. The whole mineralization cycle lasts 2-4 years only.

Conclusions

Grazing food chains based on soil algae predominate in both algal and moss communities. Trophic relations of invertebrates with algae are considered as inherited from aquatic ancestors. Green mosses are utilized by animals to a small extent and digested by means of symbiotic microorganisms. These trophic relations are regarded to be recent ones, because they are characteristic of advanced animal forms with wide enzymatic spectra, using a wide range of food sources. Moss remains are decomposed by a specific microflora. Rates of the energy flow along detrite food chains are low.

Soil animals are actively involved in detrite food chains in seed plants' communities. Saprophilic complexes reach there a maximum of taxonomic and functional diversity. The majority of saprophilic invertebrates participates in decomposition processes at the level of low predators, feeding on saprotroph microorganisms. In some animal groups trophic relations with soil microflora are replaced by mutual ones: selected microbial forms are not digested but multiply in the animal guts and their numbers in excrements are higher, than in undigested litter. It was demonstrated by studies of Diplopods, Isopods, earthworms (Kozlovskaja, 1976). Microorganisms are used by those animals as temporary symbionts. Such mutual relations are considered to represent an intermediate stage of the formation of obligate symbiosis in the course of coevolution of soil microorganisms and invertebrates. Specialized primary decomposers (Termites, woodlice, Diplopods, Tipulid larvae)have constant symbiotic complexes. The latter include bacteria, microfungi, Protozoa forming intestinal food chains. Utilization efficiency of dead plant matter reaches high values. A contribution of saprophages to primary decomposition of plant remains is characteristic of Angiosperm plants' communities. This results in an acceleration of mineralization cycle, stabilization of nutrients' supply and a qualitative increase in soil productivity.

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